Simple Models of Pattern and Process

MICHAEL BEDWARD
(Communicated by D. KEITH)

BEDWARD, M. Simple models of pattern and process. *Proc. Linn. Soc. N.S.W.*, 115: 17-23 (1995).

Pattern and process dynamics in plant communities can be modelled using cellular automata. These are simulation models that are easy to build and modify, and that are especially useful in visualizing the processes that are being modelled. To illustrate this approach, I describe a cellular automaton that simulates pattern and process in a simple bryophyte community growing on a steep rock face.

NSW National Parks and Wildlife Service, P.O. Box 1967, Hurstville N.S.W. 2220; *manuscript received 26 July 1994, accepted for publication 14 December 1994.*

KEYWORDS: Cellular automata, community population, lichen, moss.

> Come-and-go pervades everything of which we have knowledge, and though great things go more slowly, they too are built up of small ones and must fare as that which makes them.
>
> – Samuel Butler

INTRODUCTION

Pattern and process behaviour, a continual sequence of disturbance or senescence and regrowth (Watt, 1947), occurs in many types of vegetation but is particularly easy to observe in bryophyte communities that grow on steep surfaces. Ashton (1986) gives some interesting examples of pattern and process in bryophyte communities on rock faces and tree trunks. Heavy moss mats can slump from a surface creating new space that can then be colonized by algae, liverworts, lichens and eventually mosses. Moss mats may shade out and kill crustose and foliose lichens by overgrowing them. Alternatively, mosses can be parasitized and killed by lichens (McWhorter, 1921: Ashton, 1986) and the germination of moss spores can be inhibited by chemical compounds produced by lichens (Lawrey 1977). Such dynamics can produce a mosaic of different species and unoccupied space that is always shifting over time. Both the distribution and the area occupied by each species in the community can vary substantially.

One way of viewing this shifting mosaic is long term observation. Another is to attempt to model the processes involved. Modelling can also help to test the logic of our current understanding of these processes and help us to develop new hypotheses. However, there are problems in trying to construct mathematical models of these types of communities. Many of the interactions between species are very localized and spatial configuration is important. For example, the pattern of growth of a moss mat depends on the arrangement of suitable space while the pattern of moss slumping from a steep surface is influenced by how connected the moss mats are. It is usually difficult to incorporate these sort of factors into mathematical treatments (Hastings, 1991; DeAngelis and Rose, 1992).

An alternative to mathematical modelling is to use computer simulations. One very simple family of simulation models, cellular automata, have been used for a variety of ecological studies including fire patterns in vegetation (Green, 1983), the fire ecology of plant species (Green, 1985; Bradstock *et al.*, in press), host-parasite dynamics in insects (Hassell *et al.*, 1991) and evolutionary theory (e.g. Nowak and May, 1992). A cellular automaton is a collection of cells that interact in simple ways but where the whole collection can display very complex overall behaviour (Wolfram, 1984; Phipps 1992). Simulations using cellular automata proceed in discrete time steps. Each cell assumes one of a finite number of states, and its state at the next time step depends upon its current state, and the states of its neighbours. The neighbourhood of a cell can take many forms, e.g. the eight immediately adjacent cells or all cells within a specified radius, and in some models the size and shape of the neighbourhood can vary over time. The rules used to decide the state of each cell at each time step can be purely deterministic or include some element of chance (Phipps, 1992).

In this paper, I describe a cellular automaton that simulates the dynamics of a bryophyte community growing on a steep rock face. Although simple, the model displays realistic pattern and process behaviour and could easily be extended or refined to study specific communities. I have implemented the model as a computer program, MOBI (Model of Bryophyte Interactions), that displays the shifting mosaic of species and vacant space on a computer screen.

DESCRIPTION OF THE MODEL

For simplicity, the model community presented here consists of only two species: a moss and a fruticose lichen that grows upon the moss and parasitizes it. Later, I will discuss some possibilities for including further species as well as environmental variables. The habitat, a steep rock face, is represented by a square grid where each cell can be either vacant, occupied by moss, or occupied by moss and lichen. At each time step during a simulation, cells can change state according to rules that describe the growth and dispersal of the moss and the lichen, and the slumping of moss mats from the rock face. The size of the grid and the number of time steps in a simulation can vary. The temporal and spatial scale is flexible, but here I am assuming that each cell represents an area of about 1 cm^2 and each time step is about 1 year.

Moss growth and dispersal

At the beginning of a simulation, moss is assigned to a given number of randomly selected cells. The moss can then spread into adjacent cells to simulate the growth of moss clumps. The growth mechanism includes a stochastic element such that the probability of moss spreading into a vacant cell is:

$$p_{\mathrm{moss}(t+1)} = \mathrm{MAX}\ [\ 1.0\ ,\ C.f_t\ ]$$

where $p_{\mathrm{moss}(t+1)}$ is the probability of the vacant cell being occupied at the next time step; C is a constant; and f_t is the fraction of neighbours of the cell that already have moss. The neighbourhood consists of the eight immediately adjacent cells. Figure 1 shows the pattern of growth that is produced using $C = 2$.

Moss sporeling establishment was modelled by assuming that a rain of moss spores falls equally on all parts of the rock face. At each time step, moss sporelings could establish in suitable vacant cells with a specified probability that was constant throughout the simulation. Conditions on the suitability of vacant cells for sporeling establishment are explained further below.

Moss slumping

MOBI simulates the slumping of heavy moss clumps from the rock wall. To do this, each moss cell is assigned a weight. When the cell is first occupied by moss, or reoccupied after being vacant, a weight of 1 is assigned. The weight is then incremented by 1 at each time step until a preset maximum value is reached. The slumping of moss clumps is simulated at each time step by testing each moss cell to see if it will initiate a slump. The probability of this for each moss cell is equal to the weight of the moss multiplied by a constant. Cells whose weights are below a specified minimum cannot start a slump. When a falling cell is found it becomes the focus for a slump area that spreads to contiguous moss cells using the same stochastic mechanism described above for moss growth. The growth of the slump area continues until no more moss cells can be reached, or until a specified maximum area is attained, whichever happens first. Then all of the moss cells in the slump area are converted to vacant cells. A number of clumps of moss may slump from the rock face in a single time step.

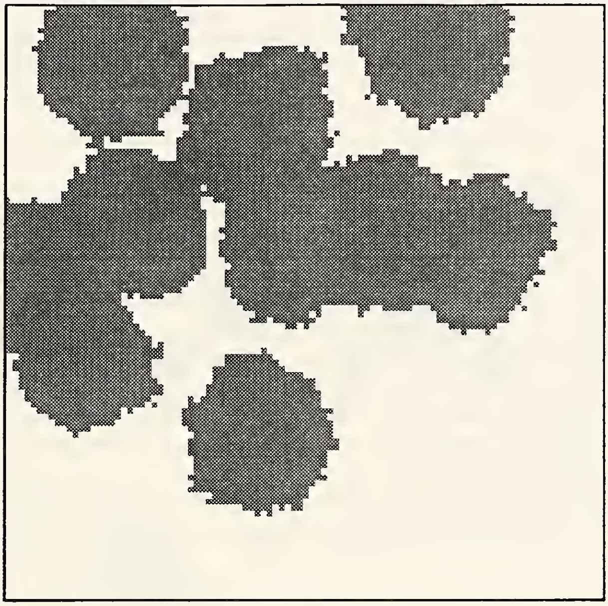

Fig. 1. Simulated moss growth from ten randomly placed initial cells in a 100x100 grid after 15 time steps.

Newly vacant cells

In some bryophyte communities, newly created space must be colonized by other species, such as algae, before moss spores can germinate and establish (e.g. Ashton, 1986). To simulate this, the number of time steps that must elapse before newly vacant cells are suitable for moss sporelings can be specified as a constant. This does not affect growth into these cells from adjacent moss clumps.

Lichen dispersal and growth

The lichen can only occupy cells that contain moss. Clumps of lichen can grow in the same stochastic manner described for moss growth. The initial lichen population is created by randomly assigning lichen to a specified number of moss cells either at the start of the simulation or at some later time. The dispersal of propagules, and establishment in moss cells, is modelled using a constant probability as for moss dispersal.

Interaction of the lichen and moss

The effect of the lichen on the moss is simply to prevent growth from infected moss cells. If all cells in a moss clump become infected the clump ceases to expand. Once infected, a moss cell can not free itself of lichen. The lichen does not affect the pattern of moss slumping. This is a very conservative and simplified interaction.

AN EXAMPLE APPLICATION

I used MOBI to see how the rate and pattern of moss mats slumping from the rock face would affect the success of the lichen. I varied moss slumping by setting four different values for the maximum area of an individual slump. I also varied moss and lichen dispersal to see what effect this would have on the behaviour of the model. Table 1 shows the design used while the complete list of MOBI variable values is given in the appendix.

TABLE 1

Number of simulations for each combination of moss slump and dispersal variables

	Maximum moss slump area (cells)			
	100	250	500	1000
Dispersal				
none	20	20	20	20
moss only	20	20	20	20
moss and lichen	20	20	20	20

Figure 2 shows the average moss and lichen populations for each set of 20 replicate simulations. As the maximum size of a slumping moss mat increased from 100 cells (fig. 2a–c) to 500 cells (fig. 2g – i) the proportion of moss infected by lichen decreased as indicated by the gap between the lines in each graph. The presence of moss and lichen dispersal made little difference to the results. Where the moss fell in very large clumps of up to 1000 cells (fig. 2j–l) dispersal had a greater effect. With neither moss or lichen dispersal (fig. 2j), both species soon became extinct. Where the moss and lichen could both disperse (fig. 2l), both persisted throughout the simulation period although only a small proportion of the moss was infected by lichen.

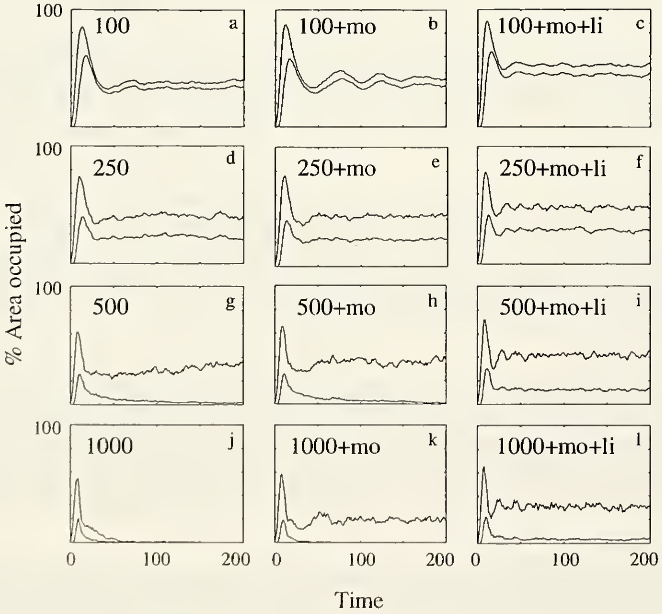

Fig. 2. Average populations of moss and lichen for each set of 20 replicate simulations (see text). In each graph, the upper line is the moss population and the lower line is the lichen population. Codes within each graph indicate the simulation settings: e.g. 100 is max slump area of 100 cells with no dispersal, 100+mo is same slump area with moss dispersal, 100+mo+li is same slump area with moss and lichen dispersal.

The mechanisms behind these results are easy to visualize by watching the moss and lichen mosaic as it unfolds in each simulation. Figure 3 shows the community in a single simulation for each level of moss slumping with no dispersal. In each simulation, 50 time steps have elapsed. Low levels of moss slumping led to small fragments of uninfected moss in a sea of lichen. When watching one of these simulations, the uninfected moss seemed to be constantly chased around the rock face by the lichen. Increasing the level of slumping led to the moss mats becoming more discrete which made it harder for the lichen to spread vegetatively. This also increased the chance of large patches of lichen being removed from the rock face. At the highest level of slumping the moss itself risked extinction when there was no dispersal.

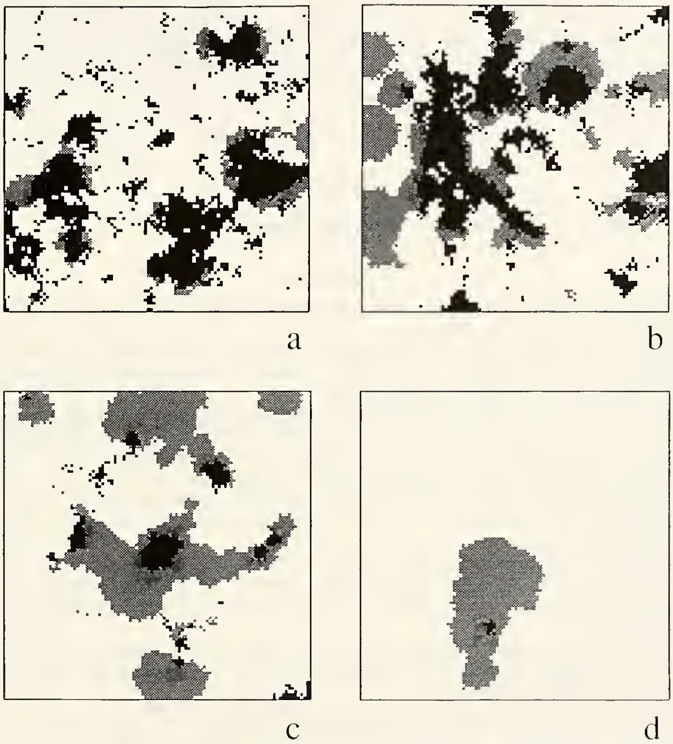

Fig. 3. The state of the model in one example simulation for each of four moss slump areas: a. 100 cells; b. 250 cells; c. 500 cells; d. 1000 cells. Grey denotes uninfected moss; black denotes moss infected by lichen.

DISCUSSION

The results show that MOBI is capable of displaying complex and realistic pattern and process behaviour. The model could be refined and extended in many ways for specific applications to bryophytic communities. For example, the probabilities for growth, dispersal and moss slumping could be linked to a historical set of rainfall data. The interaction between the moss and the lichen could be tailored to data for particular species. A simulation could also include vascular plant species that establish in moss mats and accelerate slumping of the moss when they grow large. With these sort of elaborations, MOBI could be used as a tool for population viability analysis.

Alternatively, it is possible to begin with a model such as MOBI that considers biological processes explicitly, and then simplify the model to a more abstract and general form. Hassell *et al.* (1991) took this approach with their work on insect host-parasite populations. By obtaining very similar results from models that were based on detailed mathematical formulations of species interactions, and alternative models that were purely qualitative cellular automata, they showed that it was the general pattern of species dispersal rather than the fine detail of the species interactions that determined the behaviour of the system. This sort of approach seeks to identify common patterns that underlie the behaviour of many different kinds of biological systems (e.g. Green, 1993). The results of MOBI simulations could suggest useful hypotheses for other types of plant communities that display pattern and process behaviour.

It is easy to design and build models that are based on cellular automata, such as MOBI, to explore pattern and process behaviour. Perhaps the most useful feature of these models is that you can watch the progress of each simulation and notice patterns that would not have been obvious from a mathematical treatment. This feature also makes cellular automata very useful teaching tools.

ACKNOWLEDGEMENTS

Thanks to Murray Ellis for help with the figures.

References

ASHTON, D.H. 1986. — Ecology of bryophytic communities in mature *Eucalyptus regnans* F. Muell. forest at Wallaby Creek, Victoria. *Aust. J. Bot.*, 34: 107-29.

BRADSTOCK, R.A. BEDWARD, M. and SCOTT, J.A. — *In* Press. Persistence of plant populations in landscapes subjected to recurrent fire: simulation of effects of varied frequency and size. In Proceedings of 2nd international conference on forest and fire research. Portugal.

DEANGELIS, D.L. and ROSE, K.A. 1992. — Which individual based approach is most appropriate for a given problem? *In* D.L. DEANGELIS and L.J. GROSS (eds.) Individual based models and approaches in ecology: populations, communities and ecosystems, pp. 67-87. Routledge, Chapman & Hall. New York.

CONNELL, J.H. 1978. — Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302-10.

GREEN, D.G. 1983. — Shapes of simulated fires in discrete fuels. *Ecol. Model.*, 20: 21-32.

GREEN, D.G. 1985. — Simulated effects of fire, dispersal and spatial pattern on competition with forest mosaics. *Vegetatio*, 82: 139-153.

GREEN, D.G. 1993. — Emergent behaviour in biological systems. *In* D.G. GREEN and T.J. BOSSOMAIER (eds.) Complex systems — from biology to computation, pp. 24-35. IOS Press. Amsterdam.

HASSELL, M.P., COMINS, H.N. and MAY, R.M. 1991. — Spatial structure and chaos in insect population dynamics. *Nature*, 353: 255-8.

HASTINGS, A. 1991. — Structured models of metapopulation dynamics. *Biol. J. Linn. Soc.*, 42: 57-71.

LAWREY, J.D. 1977. — Inhibition of moss spore germination by acetone extracts of terricolous *Cladonia* species. *Bull. Torrey. Bot. Club.* 104: 49-52.

MCWHORTER, F.P. 1921. — Destruction of mosses by lichens. *Bot. Gazzette*, 72: 321-5.

NOWAK, M.A. and MAY, R.M. 1992. — Evolutionary games and spatial chaos. *Nature*, 359: 826-9.

PHIPPS, M.J. 1992. — From local to global: the lesson of cellular automata. *In* D.L. DEANGELIS and L.J. GROSS (eds.) Individual based models and approaches in ecology: populations, communities and ecosystems. pp. 165-87. Routledge, Chapman & Hall. New York.

WATT, A.S. 1947. — Pattern and process in the plant community. *J. Ecol.* 35: 1-22.

WOLFRAM, S. 1984. — Cellular automata as models of complexity. *Nature*, 311: 419-24.

APPENDIX

Variables that can be set in MOBI and values used for the simulations discussed in the text.

Number of rows	100
Number of cols	100
Simulation period	200 time steps
Initial moss population	100
Initial lichen population	100
Time to add initial lichen cells	4
Lichen growth rate (relative to moss)	1
Probability of moss sporeling establishment in a vacant cell	0 or 0.001 (see text)
Probability of lichen sporeling establishment in a moss cell	0 or 0.001 (see text)
Maximum moss weight	10
Probability of any moss slippage at each time step	1.0
Minimum weight for moss to start slumping	5
Slump constant C ($prob_{slump} = C.weight$)	0.01
Maximum area of slumping moss	100 to 1000 cells (see text)
Period that newly vacant cells are unsuitable for moss sporelings	2
Moss with lichen can grow?	no